

## SEED DISPERSAL IN HYBRID *SALSOLA*

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**ABSTRACT.**— The study population is a group of hybrids of *Salsola iberica* × *S. paulsenii*. The plants show great variation in phenotypic characteristics, and the character complexes of the parent species seem to have largely disappeared. Seeds are dispersed both locally, from intact plants, and by tumbling. Tumbling is the dominant form of dispersal in most individuals studied. Most locally dispersed seeds fall between .5 and 1.5 m from the parent plant. Despite the dominance of tumbling, large numbers of seeds are dispersed locally and probably serve to maintain the population while those dispersed by tumbling introduce the plants into new areas.

Tumbling is a form of seed dispersal where the entire plant or certain parts of the plant detach and are blown along the ground by the wind, dispersing seeds with the movement. Van der Pijl (1972) mentions a number of species that disperse seeds in this manner and describes different types of modifications associated with this dispersal mode. These modifications include the upward curving of the plant to better attain a spherical shape, and methods of detachment for the tumbling parts. Becker (1978) has studied the process of detachment or abscission in *Kochia scoparia* and concludes that although the actual detachment is caused by the wind, internal desiccation of stem tissue is an important first step in this process. One of the few quantitative studies of tumbling dispersal was done on *Agrostis hiemalis* (Rabinowitz and Rapp, 1979). They showed that this grass has both stationary dispersal, when the seeds fall from the plants in place; and tumbling dispersal, during which the panicle detaches and tumbles, dispersing seeds over greater distances. Approximately half the seeds are dispersed by each mode.

One of the most commonly observed tumbling plants is *Salsola* spp., commonly known as tumbleweed or Russian thistle. This is an introduced plant in the United States, native to Eurasia. Beatley (1973) lists three species found in the U.S. and notes that the two most common, *S. paulsenii* Litv. and *S. iberica* Sennen & Pau., hybridize freely.

*Salsola iberica* is sometimes referred to as *S. kali* L. var. *tenuifolia* Tausch.

In a study of *Salsola iberica*, Evans and Young (1972) noted that seed dispersal from plants in place is slight, and concluded that tumbling is necessary for effective seed dispersal in this species. In a similar study of *S. paulsenii*, these same authors concluded that most of the seeds of this species disperse locally before the plant tumbles (Young and Evans, 1979). In both studies, seed dispersal was evaluated by taking soil and litter samples at various distances from intact plants and germinating the seeds in these samples. Our study investigates seed dispersal in a population of hybrids of these two species.

### METHODS

The population chosen for study was located in the Jones Reserve, part of the Natural Land and Water Reserve System of the University of California. This reserve is located in the Santa Monica Mountain Range, Los Angeles County, California. *Salsola* is an important part of the roadside vegetation in this area. A mile-long section of road was chosen as the study site. When the study began in October 1980, seeds were ripening on the *Salsola* in the site but little if any dispersal had occurred.

The population was sampled to determine the species of *Salsola* present. Every fifth individual along both sides of the road was

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sampled. These were taken to the laboratory and described. Beatley (1973) lists the distinguishing characteristics of *Salsola iberica* and *S. paulsenii*. We chose five of these on which to base our analysis of the study population (Table 1). Calyx size and leaf length were determined by measuring to the nearest millimeter the largest calyx and longest leaf present. Foliage color was judged by comparison of individual samples. Calyx color and stem striations were noted. Other differences between the two species mentioned by Beatley (1973) were not used because they apply only to immature plants.

The study population showed a great deal of variation in the size of individuals. To reduce this, only individuals between 1 and 1.4 meters in height were selected for the remaining parts of the research. Most of the mature individuals in the study site fell within this height range.

Eight plants were selected for local seed dispersal studies. Seed traps were constructed of petri dishes 9 cm in diameter, in which were placed filter paper covered with Tangletrap (Werner 1975). These traps were placed around the selected plants in four cardinal compass directions at the base of the plant and then at .5 m intervals to a distance of 1.5 m. Seed traps were anchored at ground level. Tall vegetation surrounding these plants and all *Salsola* within 4 m of the plant were removed. The traps were checked weekly and filter papers changed as necessary. Trapping continued until the plants broke off and tumbled, which occurred between late November and early January.

To estimate the proportion of seeds dispersed locally we chose an additional 10 individuals in the field. These plants were monitored and sampled when they were ready to

tumble. Plants were judged to be ready to tumble by pulling gently at the base. If the stem broke, the plant was sampled; if not the individual was left until a later date. For each plant, two branches were randomly chosen. The number of seeds remaining on the branch and the number of empty seed bracts were counted. These data were used to compute the proportion of seeds dispersed locally before tumbling.

RESULTS

Study Population

There was a great deal of variation in the study population in most of the phenotypic characteristics chosen for study (Table 2). The majority of the sampled plants (42 plants, 60 percent of the sample) had both pale and red stem striations, or pale striations with splotches of red at the branch nodes. These were categorized as intermediate between *Salsola iberica* and *S. paulsenii*. Only 36 percent of the sample (25 plants) had pale striations, characteristic of *S. paulsenii*, and 4 percent (3 plants) had all red purple striations, characteristic of *S. iberica*.

Calyx color in all sampled individuals was pale or pale with some red near the base of the calyx wings, and all were categorized as *S. paulsenii* in this characteristic. Foliage color was more variable. Forty-four percent (31 plants) had blue green foliage and were categorized as *S. iberica*, 29 percent of the sample (20 plants) were judged to have yellow green foliage (*S. paulsenii*), and 27 percent (19 plants) were intermediate.

Calyx size varied between 2.5 and 4 mm but on most plants fell between 3 and 3.5 mm. The calyx of *S. iberica* is usually less

TABLE 1. Distinguishing characteristics, *Salsola paulsenii* v. *S. iberica*<sup>a</sup>.

Character	<i>S. paulsenii</i>	<i>S. iberica</i>
Plant color	Yellow green	Blue green
Stem striations	Pale or none	Red purple
Calyx color	Colorless or pale pink, usually red near base of wings	Deep red
Calyx size	3-4 mm	2 mm
Leaf length	.5-1.5 cm	2 cm

<sup>a</sup>After Beatley, 1973.

TABLE 2. Characteristics of the study population.

Character	Percentage of sampled individuals <sup>a</sup>		
	<i>S. paulsenii</i>	Intermediate	<i>S. iberica</i>
Stem striations	36	60	4
Calyx color	100	0	0
Foliage color	29	27	44
Calyx size	63	37	0
Leaf length	61	0	39

<sup>a</sup>Total number of plants sampled = 70.

than 2 mm (Beatley 1973), so all the individuals sampled appeared to be either intermediate between the two species, or *S. paulsenii*, which has calyx wings of 3 to 4 mm.

Leaf length showed a pattern of variation similar to calyx size. Leaves varied between .6 and 3.7 cm, but the majority of the sample fell between 1 and 2.3 cm. Thirty-nine percent of the sample had leaves of 1.5 cm or less and were classified as *S. iberica*; the remainder were categorized as *S. paulsenii*.

These characteristics do not seem closely linked in individuals (Fig. 1). Individuals with yellow green foliage seem somewhat more likely to have calyxes of 3.5 mm and leaves of about 1 cm (all *S. paulsenii* characteristics) and those with blue green foliage tend to have *S. iberica* characteristics in leaf length and calyx size. But this is an extremely weak trend and is largely overshadowed by the great variation in most of the characteristics. These results seem to indicate that the population is made up of hybrids of these two species. It is probably an old, established hybrid population in which the character complexes

of the original species have largely disappeared.

Pattern of Local Seed Dispersal

Seed traps placed around eight individuals were used to determine the pattern of local seed dispersal. The average number of seeds trapped at each distance for each plant is shown in Figure 2. Two types of patterns can be seen in these graphs. Most of the individuals (Nos. 2, 3, 6, 7, 8) show a general decrease in density of seed dispersal with increasing distance from the plant. In one of these individuals (Plant No. 8), traps at .5 m caught more seeds than those at the base of the plant, but the density of seed fall then decreased with distance. Although the size of the plants varied somewhat, traps at .5 m were in all cases under the canopy of the plant, usually quite close to the edge of the canopy, and those at 1 m were outside the canopy. These individuals then show more dense seed dispersal under the canopy with decreasing seed density at increasing

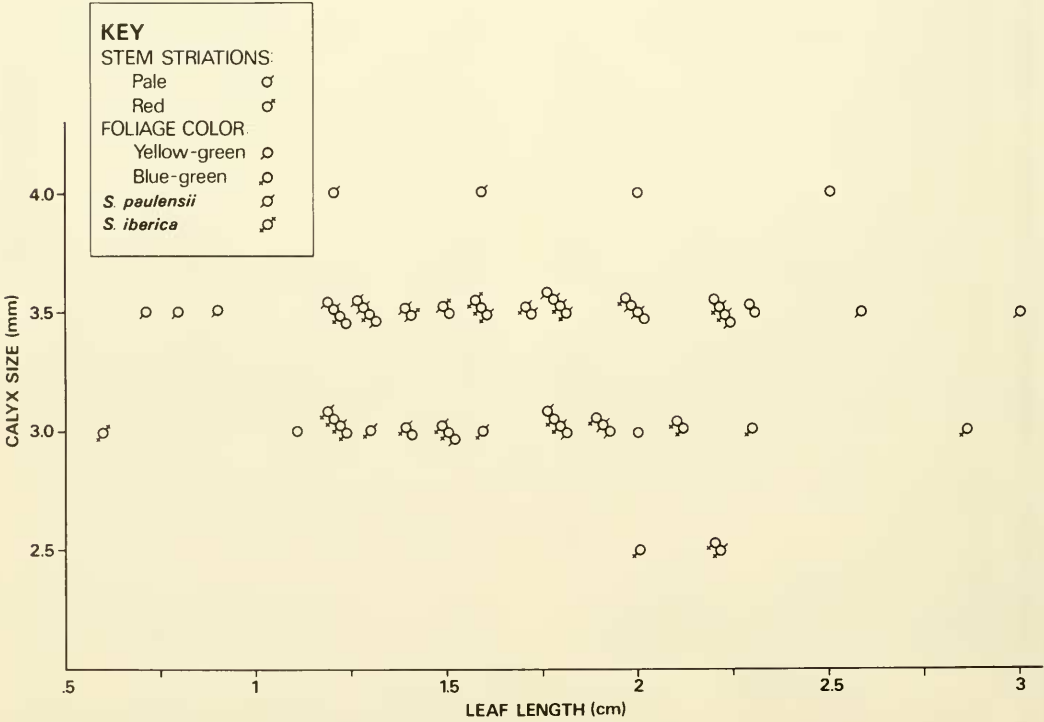


Fig. 1. Scatter diagram showing characteristics of study population. Each dot represents one sampled plant. Stem striations and foliage color shown as oblique lines and crosses. Lack of these symbols indicates intermediate characteristics as explained in the text.

distance. Plants 4 and 5 have a somewhat different pattern. Here seeds are more densely dispersed at 1 m than under the canopy. In both these generalized patterns, few seeds were caught at 1.5 m. Plant No. 1 is anomalous in that seed density increases with increasing distance.

These data describe only the density of seed fall at a given distance from the plant, not the actual number of seeds that fall at that distance. The total number of seeds that disperse within a given distance can be computed only by taking into consideration the size of the area. In a circular formation such as that represented by these seed traps, the area in each distance interval varies greatly. For example, the circle around the plant formed by the traps placed at the base of the plant has an area of .0254 m<sup>2</sup>. The most distant traps, placed at 1.5 m from the plant, sample a ring-shaped area, .5 m in width, with a total area of 3.972 m<sup>2</sup>. Additionally, these traps sample seed fall density only at

the edges of these rings, and the density obviously changes over the interval. To compute the number of seeds that fall at each distance, a dispersal curve was drawn for each distance interval, using the average number of seeds caught at each distance as the end points. This curve was then rotated 360 degrees around the origin (base of the plant) to produce a solid. The volume of this solid was computed to estimate the total number of seeds that fell into the area. For this analysis, it was assumed that seeds were not dispersed beyond 2 m from the parent plant, and the dispersal curve was extended to 0 seeds at a distance of 2 m.

When this procedure is followed, the local dispersal patterns are changed somewhat (Fig. 3). In all cases more seeds fell between .5 and 1 m than fell directly under the plant (between the base and .5 m). Between 1 and 1.5 m seed fall varies. For some individuals it is greater than at closer distances; in others it is smaller. Between 1.5 and 2 m total seed

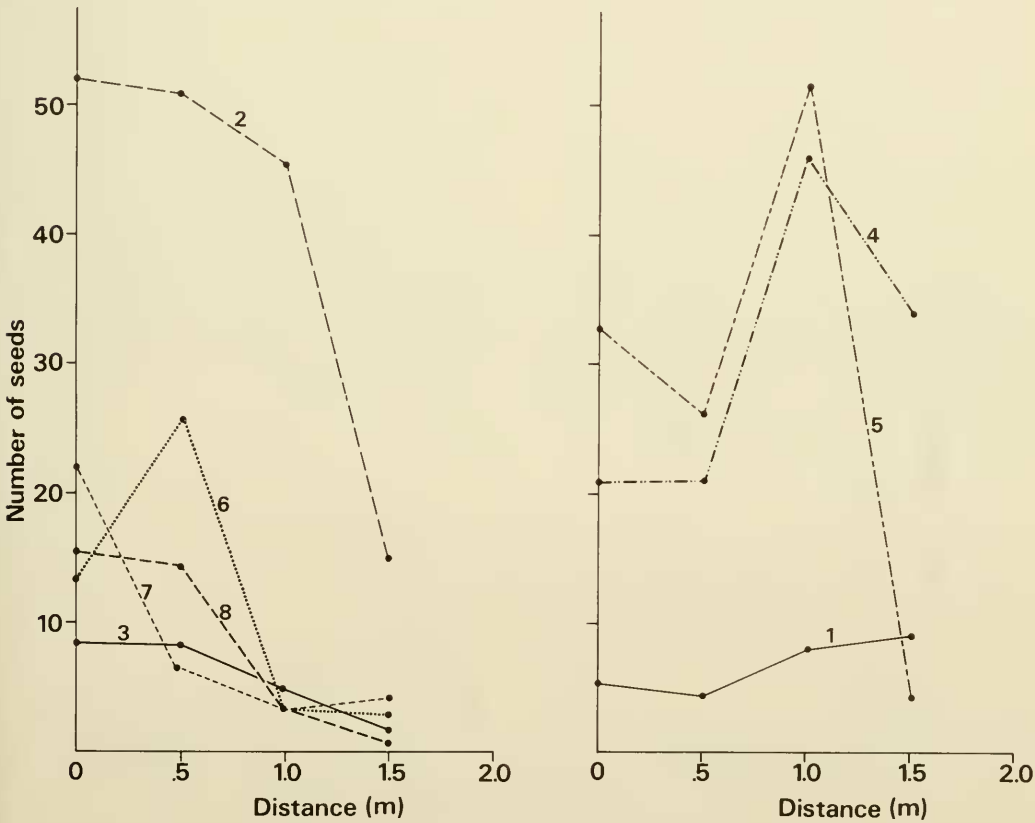


Fig. 2. Average number of seeds caught in traps placed around eight plants. Each plant is shown separately. Four traps were placed at each distance, as described in the text.

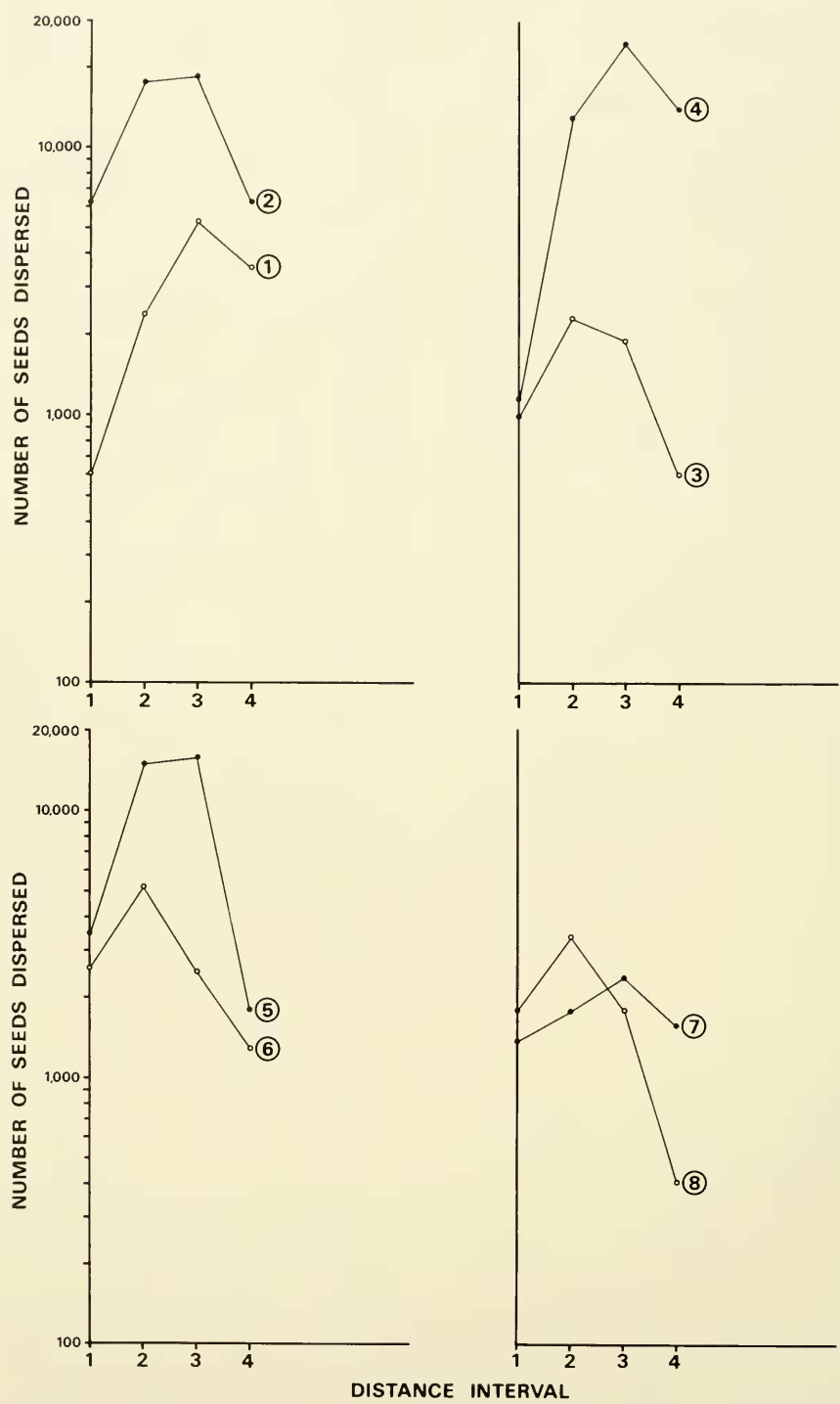


Fig. 3. Total number of seeds (on a logarithmic scale) dispersed in each distance interval. Each plant is shown separately. The method for determining total seed fall based on samples from seed traps is explained in the text.



fall also varies, but it is always less than the previous interval. In several cases (e.g., Nos. 1, 4, 5), however, seed fall in the most distant area is actually greater than directly under the plant.

The proportion of locally dispersed seeds in each distance interval is shown in Table 3. In all cases 60 percent or more of the seeds fall between .5 and 1.5 m from the plant. The proportions falling closer to the plant, at distances up to .5 m, and further away (between 1.5 and 2 m) show more variation among the individuals sampled.

The heavy seed fall between .5 and 1.5 m is probably in part a result of the fact that more seeds are borne toward the branch tips than near the stem. There is obviously some lateral movement of seeds, probably enhanced by wind.

Importance of Local Dispersal

The importance of local seed dispersal was evaluated by counting the number of empty seed bracts and the number of seeds remaining on two branches of each of 10 individuals. The proportion of seeds falling before tumbling ranged from 12 to 64 percent, with a mean value of 29.5 percent (Fig. 4). Five of the 10 sampled plants dispersed between 20 and 30 percent of their seeds before tumbling. Only two plants dispersed less than 20 percent locally, and only one dispersed more than 50 percent of its seeds locally. Tumbling then remains an important mode of seed dispersal in this hybrid population.

Although a relatively low proportion of the seeds are dispersed in the immediate area of the parent plant, this proportion represents a large number of seeds. Total number of locally dispersed seeds, as estimated from the dispersal curves, is shown in Table 3. These estimates vary among the individuals, but even the smallest, plant No. 3, is slightly over 6,000 seeds.

CONCLUSIONS

The study population is a group of hybrid individuals of *Salsola paulsenii* × *S. iberica*. Individual plants show wide phenotypic variation. It is apparently an old population in which the original character complexes have disappeared.

Seeds from these plants are dispersed both locally, from intact plants, and by tumbling. Although there is some variation among the individuals in the importance of these two modes, most sampled plants disperse 30 percent or less of their seeds locally. Patterns of local seed dispersal indicate that the largest proportion of these seeds (60 percent or more) fall between .5 and 1.5 m from the parent plant. These results contrast with those found in *Agrostis hiemalis*, a grass that also has dual dispersal modes. In that species local dispersal and tumbling are about equally important in terms of the proportion of seeds dispersed, and locally dispersed seeds fall closer to the parent plant, about 50 percent within .46 m (Rabinowitz and Rapp 1979).

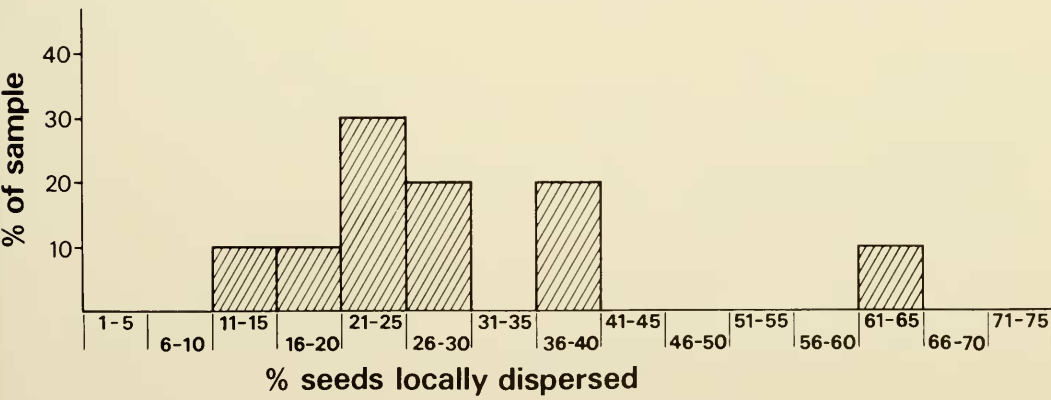


Fig. 4. Proportion of seeds dispersed locally. Data are given as average percentage of seeds dispersed before tumbling for ten sampled plants.

TABLE 3. Proportion of locally dispersed seeds in each distance interval.

Plant number	Percent of seeds in each interval				Total number of seeds dispersed locally
	0-.5m	.5-1m	1-1.5m	1.5-2m	
1	5.2	20.5	43.8	30.4	11,831
2	13.0	36.6	37.4	13.0	48,557
3	17.1	38.7	32.3	11.9	6,028
4	4.8	23.9	45.3	26.0	54,506
5	9.6	40.8	44.6	5.0	36,618
6	22.4	44.5	21.5	11.6	11,745
7	19.7	25.1	32.7	22.5	7,325
8	24.0	45.7	24.8	5.5	7,530

The dual dispersal modes exhibited by these hybrids is apparently a combination of the principal dispersal strategies used by the two parent species. *Salsola iberica* disperses seed mainly by tumbling, and *S. paulsenii* is more heavily dependent upon local dispersal (Young and Evans 1979, Evans and Young 1972). Although tumbling appears to be the dominant method in this hybrid population, the large number of seeds produced by these plants suggest that significant numbers of seeds are dispersed in the immediate area of the parent plant. These seeds probably serve to maintain the population, and those dispersed by tumbling spread the species to new areas.

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